

17. Notes on the Respiratory Mechanism of the Ampullariidæ.

By GUY C. ROBSON, M.A., F.Z.S.

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During the latter part of the last century a good deal of work was done upon the respiration of the amphibious gastropod *Ampullaria*. The studies of Bavay, Sabatier, Bouvier and Fischer together with the more recent work of Ramanan yielded a satisfactory general account of the process. The method by which the gill and lung are alternatively employed, the conditions under which one or the other becomes functional and the relation of the circulation to the respiratory organs are therefore fairly well known. There are, however, several details upon which the older accounts are vague, and certain features seemed so inexplicable that the donation by Colonel Knight and Colonel Porteous of living examples of *A. vermiformis* to the Society, afforded a very welcome opportunity for fresh study.

The general phenomena of pulmonary and branchial respiration recorded by Jourdain (6), Bouvier and Fischer (3), and Bavay (1) for various Neotropical forms are found to take place in *A. vermiformis*. There is no need, therefore, to describe the details which may be found in the two latter papers. Bavay described three types of respiration, and I propose to use the term 'siphonal' for the one in which air is drawn into the lung through the siphon while the animal is still under water. It is to be distinguished from ordinary branchial respiration on the one hand and from direct pulmonary respiration on the other.

A. The first point upon which fresh evidence may be offered is the function of the longitudinal ridge ('repli palléal') which sub-divides the pallial cavity. Jourdain, Bavay and others speak as though the pallial cavity were divided into two separate parts by the ridge in question which runs up the floor of the cavity parallel to and on the left-hand side of the gill and rectum. The precise rôle of such a division is not specified by previous workers; but one is left with the distinct impression that this apparent division of the mantle-cavity into right (branchial) and left (pulmonary) areas is of importance in respiration. The available facts, however, appear to indicate that this is not the case. To seal effectually the 'pulmonary' pallial chamber from water or the branchial chamber from air, the separation of the two chambers should be complete. But in over twenty examples of various species and genera I have never found the ridge nearly high enough along its entire length to touch the pallial roof. Bavay,

on the other hand, says that it fits into a groove in the latter. It is possible that, in the spirit specimens I have examined, the ridge is contracted and drawn away from the roof of the pallial cavity.

In the first place it is unfortunate that we can have no direct evidence on this subject. In a living animal we are obviously unable to see whether the pallial roof is in contact with the entire length of the ridge. We have, therefore, to fall back upon indirect evidence. The following facts appear to indicate that the separation is not complete. The ridge is sometimes quite high enough anteriorly to touch the roof of the cavity; but it almost invariably decreases in height posteriorly so that it is difficult to see how complete insulation of the two chambers can be thereby effected. Secondly, I have never found a groove deep enough to hold the top of the ridge steady against the pressure of water. Thirdly, I have frequently found the albumen gland so much distended that it presses down a portion of the ridge and keeps the pallial roof away from it, thus opening a more complete communication between the two cavities. Finally, there can be no actual need to prevent water from entering the so-called pulmonary pallial cavity from the side of the gill, as it may be seen frequently entering it from the left-hand side. It is, perhaps, from this latter fact that we may derive an explanation of the function of the ridge. Water apparently enters the pallial cavity from the left-hand side, passes backwards, and then is passed forwards over the gill to be finally discharged from the right-hand side. It seems likely that the ridge functions in guiding the current of water, and its structure (usually high anteriorly and diminishing in size posteriorly) is in accordance with such a function. The criticism will at once suggest itself that similar arrangements for directing the current of water in branchial respiration are not found in the large assemblage of other Prosobranchs which employ branchial respiration. Difficult as this argument may be, it appears to offer less obstacles to a solution than the fact that a similar ridge is found in *Vivipara* in which no lung is found!

The function of the ridge in that genus has been discussed by Sewell (9), who regards it as 'respiratory,' though he does not make its precise rôle clear. The possibility that the ridge may form part of a gutter down which the renal excretions pass to the exterior should not be overlooked. Bouvier (2) suggests that it acts in this capacity in *Ampullaria*, as a result of the displacement of the gill into the area of renal excretion. It should not be overlooked, however, that the ridge is found in *Vivipara* in which there is a fully-formed ureter as well!

B. The next point of interest is whether during siphonal respiration there is a direct connection between the base of the siphon on its inner side and the orifice of the lung. It must be admitted in advance that the evidence to be adduced is mainly

negative; but as the question is very obscure and at the same time connected with the whole question of the respiratory mechanism, we may attempt to make the issue a little clearer.

Bavay and Bouvier (2*a*) imply that the siphon and respiratory orifice form a continuous tube. If this is the case, the air from the exterior passes down the siphon straight into the lung and none of it is wasted in the pallial cavity. As to the details, Bouvier is the more explicit. After admitting that during the act of siphonal breathing it is impossible to see what is going on in the pallial cavity, he says that afterwards the 'plancher pulmonaire' becomes visible (*i.e.* by the modification of the shape of the siphon and its base) and that it is "susceptible de faire saillie en avant jusqu'au voisinage de la base du siphon." The chief thing to notice is that during the actual process of siphonal breathing it is impossible to see what is going on inside the pallial cavity. It is a controversial point whether one is entitled to assume that siphon and pulmonary orifice are continuous at a given moment because a little while afterwards the latter is found projecting towards the former! It is thus difficult to see on what critical facts Bouvier and Bavay based their statements. As far as *A. vermiciformis* is concerned, even if it is seized during siphonal breathing and the pallial cavity forced open, the siphon resumes its normal shape before the base and respiratory orifice come into view.

A priori one would be tempted to assume that the connection in question is necessary. It would be physiologically advantageous to have a means whereby the air is conveyed straight into the lung and not wasted in the pallial cavity. It might also be desirable to keep air away from the gill. But we may point out (*a*) that the siphon is not used at all in direct pulmonary breathing, so that the question of physiological economy does not seem to be involved, and (*b*) that during siphonal respiration the mantle cavity is kept tightly closed by the down-drawing of the mantle folds, so that there is no risk of water entering the cavity and finding its way into the lung.

C. A comparison of the observations upon Neotropical forms with those published by Ramanan (7) upon the Oriental *Pachylabra globosa* and by Bouvier and Fischer upon the Egyptian *Lanistes bolteniana*, suggests that the structural differences upon which Fischer (5) separated the American, Indian, and African forms are correlated with differences in the mode of respiration.

Fischer divides the Ampullariidæ into the following genera:—

1. *Ampullaria* s. s. including *Marisa* (= *Ceratodes*): siphon very long. America.
2. *Pachylabra*: siphon rudimentary. Africa, Asia, Oceania.
3. *Asolene*: siphon absent. South America.
4. *Lanistes*: (siphon?). Africa, Madagascar.
5. *Meladomus*: (siphon?). Africa.

It is desirable to know to what extent the differences illustrated by his classification are to be found in other features of the respiratory system.

In order to test this I have examined the respiratory organs of the following forms, all of which are represented in the material available in the Zoological Department of the British Museum:—

1. *Marisa cornu-arietis* (Trinidad).
2. *Ampullaria vermiformis* (Pernambuco).
3. „ *glauca* (Demerara).
4. „ *insularum* (South America, ? loc.).
5. *Lanistes affinis* (Victoria Falls).
6. „ *olivieri* (Egypt).
7. *Pachylabra* sp. (Sikkim).
8. „ sp. (Perak).
9. „ *gordoni* (Victoria Nyanza).

According to Bouvier and Fischer (3) *Lanistes* is less specialized for siphonal respiration than *Ampullaria*. The siphon is short and does not appear to form a complete tube. On coming to the surface of the water it apparently places its respiratory orifice in direct communication with the air, and the siphon is not an indispensable part of the mechanism. *A.* (= *Pachylabra*) *glauca*, to judge from Ramanan's account, represents a more advanced condition, but not yet approximating to *Ampullaria* s. s. There is true siphonal respiration and apparently, as in the South American *vermiformis*, the base of the siphon assists in closing the left-hand side of the pallial aperture. But the siphon is very short, its orifice very broad, and there is no pumping-movement of the head such as Bavay and others have described for South American forms and as Miss Cheesman and I have witnessed in *A. vermiformis*. We finally have complete siphonal breathing in *Ampullaria* s. s. achieved by a very long flexible siphon.

In *Ampullaria* and *Marisa* there is a rather small and sub-circular or ovoid respiratory orifice situated on the anterior end of the lung-cavity rather towards the left. Its edges are sometimes thickened slightly and tend to overlap each other. It is difficult to see whether closure is effected by a sphincter or by the overlapping edges.

In the two Asiatic species examined and in *P. gordoni* from East Africa a very different condition is found. The respiratory aperture is large and gaping, and is not a simple orifice in the floor of the lung. Generally found more in the middle of the latter, it extends backwards and to the right—as far as the right-hand wall of the pulmonary cavity—as a wide longitudinal slit between two markedly overlapping edges, the inferior of which (left-hand) is inserted into the floor of the pallial cavity.

In *Lanistes* the orifice occupies more or less the same position as in *Ampullaria*, i.e. anterior, to the left and close to the osphradium. It shows, however, the same general structure as in

Pachylabra, though an individual feature is seen in the development of an upraised ridge on the right-hand edge. The orifice is almost as long as in *Pachylabra*, but in the two species examined it does not extend so far backwards.

It is impossible as yet to discuss the course of evolution in the Ampullariidæ. It would seem, however, that the method of respiration and the structure of the siphon and the respiratory orifice exhibit a correlated and progressive modification. At first the siphon is short and almost functionless, the respiratory orifice elongate. Then the siphon acquires an intimate association with the left-hand side of the pallial aperture which it assists to close during siphonal respiration. It increases in length and can become completely tubular. The respiratory orifice becomes restricted in size and anterior in position and possibly more directly approximated to the base of the siphon.

D. The development of the lung-cavity* from the branchial chamber in the Ampullariidæ is comparable to the similar phenomenon in *Birgus latro* and the terrestrial Brachyura and in certain gobiid fishes, and the amphibious habits of these animals are in general alike. Semper (8) and others have dealt with the causes which may lead to the development of the amphibious habit, so that there is no need to discuss this matter in detail. It might be pointed out that in the case of *Ampullaria* the development of a lung is apparently not necessarily connected with the periodic drying-up of the streams and the sheets of water in which the molluscs live. *Ampullaria*, to judge from numerous observations, is capable of spending a long period in a state of reduced metabolism familiar to all students of molluscan æstivation. This process is of course facilitated in operculate forms by the retention of moisture in the tissues owing to the complete insulation of the animal by the operculum. The methods by which the Ampullariidæ are able to resist the annual periods of desiccation are, therefore, probably the same as that of other tropical molluscs. The significance of the development of the siphon is quite a different matter. The development of the siphon is probably correlated with an increased tendency to live in streams covered with a dense mat of surface vegetation in which the short siphonal forms could not exist. In drawing attention to a possible adaptational value of the siphon, I do not wish to assert that it was necessarily adaptive in its origin.

I am indebted to my friend Dr. Baini Prashad of the Zoological Survey of India for permission to state that, so far as *Pachylabra* is concerned, his views (arrived at independently) with regard to the adaptational value of the long siphon are the same as those advanced above.

* It is interesting to note that Brooks and McGlone (4), who have studied the development of the North American *A. depressa*, find that the lung-cavity is developed as an infolding between the ridges from which the gill and osphradium are developed, all three structures arising from practically the same area in the embryonic mantle-cavity.

I have also to express my obligation to Miss E. Cheesman for facilitating my observations on the animals placed under her charge and for several valuable suggestions.

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